Reproduction in an Introduced Population of the Brown Anole, *Anolis sagrei*, from O'ahu, Hawai'i[1]

Stephen R. Goldberg,[2] *Fred Kraus,*[3] *and Charles R. Bursey*[4]

Abstract: The reproductive cycle of an introduced population of the brown anole, *Anolis sagrei*, from O'ahu, Hawai'i, was studied from a histological examination of monthly samples collected July 1999 to June 2000. Males undergo a seasonal testicular cycle in which all males > 38 mm snout-vent length are in spermiogenesis from January to August. Although some ovarian activity was found in all months, the period of greatest ovarian inactivity was October–December, which corresponds to the time of male gonadal regression. The reproductive cycle of *A. sagrei* in Hawai'i resembles that of populations in Belize, Florida, and Jamaica, where minimum gonadal activity was recorded from November through February. Body sizes at reproductive maturity were similar in all four localities. *Anolis sagrei* in Hawai'i has an ovarian cycle typical of other *Anolis* lizards with a prolonged breeding season and production of single eggs in succession. Because *A. sagrei* has been in Hawai'i for only approximately 20 yr, sufficient time has not elapsed to allow evolution of its reproductive cycles, but this study presents baseline reproductive data that can be used for future studies to see if the *A. sagrei* reproductive cycles are modified as the lizards adapt to the environmental conditions of their newly colonized range.

THE BROWN ANOLE, *Anolis sagrei* Duméril & Bibron, 1837, was originally known from Cuba, Jamaica, the Bahamas, the Atlantic coast of Mexico to Belize (Schwartz and Henderson 1991), and has been introduced to the Cayman Islands (Minton and Minton 1984, Franz et al. 1987), Hawai'i (Kishinami and Kishinami 1996, McKeown 1996), and Florida (King and Krakauer 1966). From Florida, the species has subsequently spread to Georgia (Campbell and Hammontree 1995, Echternacht et al. 1995, Campbell 1996), Louisiana (Thomas et al. 1990, Platt and Fontenot 1994), and Texas (Dixon 1987, King et al. 1987, Krusling et al. 1995) and has appeared adventitiously in Virginia (Mitchell 1982, 1994).

The origin of the Hawaiian population is unknown, but it is believed that these anoles are descendents of released pets (McKeown 1996), although importation as hitchhikers on nursery materials cannot be ruled out (Kraus in press). In either case, the provenance of this population is probably Florida. The species was first noticed in 1980 and is still largely restricted to residential and urban areas, occurring only on O'ahu. Because of the demonstrated invasiveness of *A. sagrei* in the southeastern United States, its tolerance of harsh temperature regimes, and formation of dense populations, this species has the potential to exert negative effects on Hawai'i's remaining native low-elevation insect fauna. This concern is supported by documentation of direct and indirect effects of experimentally introduced populations of *A. sagrei* on arthropod communities (Schoener and Spiller 1999). Despite this potential and the species'

[1] Manuscript accepted 21 August 2001.

[2] Corresponding author, Department of Biology, Whittier College, Whittier, California 90608 (E-mail: sgoldberg@whittier.edu).

[3] Department of Land and Natural Resources, Division of Forestry and Wildlife, 1151 Punchbowl Street, Honolulu, Hawai'i 96813. Current address: Department of Natural Sciences, Bishop Museum, 1525 Bernice Street, Honolulu, Hawai'i 96817.

[4] Department of Biology, Pennsylvania State University, Shenango Campus, Sharon, Pennsylvania 16146.

Pacific Science (2002), vol. 56, no. 2:163–168

prominence where established on O'ahu, basic information on the ecology of this invasive species in Hawai'i is absent.

Reproduction of *A. sagrei* has been studied in Belize, Florida, and Jamaica (Licht and Gorman 1970, Sexton and Brown 1977, Lee et al. 1989). The purpose of the study reported here was to describe the reproductive cycle of *A. sagrei* from O'ahu, Hawai'i, so as to compare its reproductive pattern with those of *A. sagrei* from other locations and to provide some of the ecological information necessary for evaluating the threat these lizards pose to native Hawaiian ecosystems. Because Hawai'i differs from Florida and the Caribbean in some climatic variables such as rainfall, temperature, and photoperiod that may be relevant for cuing reproductive cycles, our data further serve as a baseline to assess the degree to which the reproductive cycles of *A. sagrei* will change in the future in response to the different climatic regime of Hawai'i.

MATERIALS AND METHODS

Monthly samples of approximately 20 *A. sagrei* (total = 126 females, mean snout-vent length (SVL) = 42 mm ± 5 SD, range = 21–51 mm; 138 males, mean SVL = 53 mm ± 7 SD, range = 31–66 mm) were collected by hand near Kailua (21° 25′ N, 157° 45′ W) on the windward side of O'ahu between 1 July 1999 and 30 June 2000. The lizards were killed by immersion in chloretone, fixed in neutral buffered 10% formalin, preserved in 70% ethanol, and shipped to Whittier, California, for examination. Sizes of both testes in each male were similar, indicating they were at the same stage of the male cycle. The left testis was removed for histology. In females, left ovaries with follicles <3 mm diameter were removed for histology; ovaries >3 mm were left in situ and the number of follicles counted. Because the chances of follicles >3 mm ovulating was high, counting them gave an accurate estimation of clutch size. Oviductal eggs were also counted when present. Tissues were dehydrated in an ascending series of ethanol, embedded in paraffin, and sections were cut at 5 μm and mounted on glass slides. Sections were stained in Harris' hematoxylin followed by eosin counterstain. Lizards were subsequently deposited in the herpetology collection of the University of Michigan (UMMZ) Museum of Zoology, Ann Arbor, Michigan.

Testicular tissue was examined microscopically, and each sample was assigned to one of three stages in the testicular cycle: (1) regressed—seminiferous tubules contained spermatogonia and Sertoli cells only; (2) recrudescent—seminiferous tubules exhibited markedly increased cellularity with primary spermatocytes predominating; (3) spermiogeneic—sperm, spermatids, and metamorphosing spermatids abundant. Similarly, ovarian tissue samples were assigned to one of four stages of the ovarian cycle: (1) inactive—no yolk deposition; (2) yolk deposition in one or more ovarian follicles; (3) oviductal eggs present and yolk deposition in one or more ovarian follicles; (4) oviductal eggs present, no yolk deposition in ovarian follicles.

Sexual differences in lizard body sizes were compared by a Kruskal-Wallis test, monthly differences in ovarian activity were compared using chi-square tests, and periods of male and female reproductive activity were examined by correlation analysis (Campbell 1989).

RESULTS

Examination of gonads revealed males of <38 mm SVL and females of <35 mm SVL to be immature; immature animals were excluded from reproductive analyses. Thus, analyses included 113 adult females (SVL = 43 mm ± 3 SD, range = 35–51 mm) and 133 males (SVL = 55 mm ± 6 SD, range = 38–66 mm). Males were significantly larger than females (Kruskal-Wallis test = 54, df = 1, $P < 0.001$).

Males of *A. sagrei* were found to undergo a seasonal testicular cycle (Table 1). From January to August, all adult males were found to be in spermiogenesis. Males with regressed testes were found only from September to November ($n = 13$ of 34, 38%); males in recrudescence were found in September, November, and December ($n = 19$ of 45, 42%). However, even during these months,

TABLE 1

Stages in Testicular Cycle of *Anolis sagrei* from July 1999 to June 2000 from O'ahu, Hawai'i

Month	*n*	No. Individuals with Regressed Testes	No. Individuals with Recrudescent Testes	No. Individuals with Spermiogenic Testes
July	9	0	0	9
August	10	0	0	10
September	9	2	1	6
October	6	5	0	1
November	19	6	5	8
December	17	0	13	4
January	11	0	0	11
February	10	0	0	10
March	9	0	0	9
April	12	0	0	12
May	11	0	0	11
June	9	0	0	9
Total	133	13	19	101

TABLE 2

Stages in Ovarian Cycle of *Anolis sagrei* from July 1999 to June 2000 from O'ahu, Hawai'i

		No. of Individuals with Ovary Condition[a]			
Month	*n*	Inactive	Yolk Deposition	Oviductal Eggs and Yolk Deposition	Oviductal Eggs and No Yolk Deposition
July	9	1	0	6	2
August	10	1	1	2	6
September	10	3	3	1	3
October	9	7	2	0	0
November	7	4	2	0	1
December	7	5	2	0	0
January	5	1	3	1	0
February	10	0	4	6	0
March	11	1	2	8	0
April	10	2	0	8	0
May	11	0	1	10	0
June	14	0	5	9	0
Total	113	25	24	52	12

[a] See Materials and Methods.

some males were undergoing spermiogenesis ($n = 19$ of 51, 37%).

A seasonal ovarian cycle in females of *A. sagrei* was less obvious (Table 2). For adult females, yolk deposition and/or oviductal eggs were found in all months ($n = 88$ of 113, 78%). There were females with oviductal eggs that had commenced yolk deposition for a subsequent egg clutch (basophilic vitellogenic granules present) during all months except October–December, indicating that a portion of the female population produced successive egg clutches during the reproductive season. In 17 of 63 (27%) oviductal females, two eggs were present and in 1 of 63 (2%) three eggs were present. However, in such cases, one oviductal egg typically had a thicker shell than the other, suggesting that

there was a time period between ovipositions, with one egg deposited at a time. Ovarian inactivity was found in all months except February, May, and June ($n = 25$ of 113, 22%). However, greatest ovarian inactivity was in September–December; inactivity during this period was significantly greater than inactivity during the rest of the year when compared in the 4-month sequences January–April and May–August (chi square = 34, df = 2, $P < 0.001$). One female each from October, November, and December that had initiated yolk deposition was undergoing follicular atresia, a process in which granulosa cells that surround the interior of the follicle enlarge and engulf yolk (Goldberg 1970). Follicular atresia most commonly occurs at the end of the reproductive season (Goldberg 1973, 1975). The 4-month time period of the regressed testicular condition of males correlated well with the 4-month time period of ovarian inactivity of females ($r = 0.83$, df = 1, $P > 0.05$). Neonates were observed from late June through September in 1999, but as early as mid-April in 2001.

DISCUSSION

The reproductive cycle of *A. sagrei* in Hawai'i (minimum gonad activity October–December) resembles that of populations in Belize, Florida, and Jamaica, where minimum gonad activity was recorded from November through February (Licht and Gorman 1970, Sexton and Brown 1977, Lee et al. 1989). In all studied populations of *A. sagrei* the reproductive cycles were seasonal. Likewise, SVL at initiation of spermiogenesis and oogenesis is similar in all four locations: Hawai'i, males 38 mm, females 35 mm; Belize, males 40 mm, females 39 mm; Florida, males 39 mm, females 34 mm; Jamaica, males 35 mm, females 34 mm (Licht and Gorman 1970, Sexton and Brown 1977, Lee et al. 1989). Last, the ovarian cycle of *A. sagrei* (in all locations) follows the pattern described for other female *Anolis* lizards in which there is a prolonged breeding season with production of single eggs in regular succession (Hamlett 1952, Licht and Gorman 1970). This prolonged period of ovarian activity differs markedly from that of temperate-zone lizards, where eggs are produced only during a limited part of the year (Goldberg 1972, 1973, 1975).

Fitch (1982) found reproduction of tropical anoles to correlate generally with the rainy season. Lee et al. (1989) interpreted this rough synchrony between reproduction and rainfall as an adaptation that results in deposition and development of eggs under suitable hydric conditions. Miami, Florida, the study area of Lee et al. (1989), is characterized by dry winters and wet summers (U.S. Department of Commerce 1975–2000*a*). Egg production of *A. sagrei* occurred during the wet summer in Florida (Lee et al. 1989). Similarly, Licht and Gorman (1970) and Sexton and Brown (1977) reported fewer reproductive *A. sagrei* females during the dry winter than in the wet summer in Jamaica and Belize, respectively. Kailua, O'ahu, Hawai'i, has the reverse rainfall pattern of Florida, Jamaica, and Belize, with a wet winter/dry summer (U.S. Department of Commerce 1975–2000*b*). The period of minimum female reproductive inactivity in *A. sagrei* occurs during the wet season, contrary to the expectations of Lee et al. (1989). If the presence of rainfall is important for successful egg production in *A. sagrei*, one might expect a shift in the female reproductive cycle in Hawai'i to allow for increased winter (wet period) egg deposition and a concomitant decrease in summer (dry period) egg deposition. Our data, 20 yr into the invasion process, indicate no such shift yet, but they serve as a baseline for future studies investigating such a shift. Any effects that rainfall patterns might be having on the timing of lizard reproductive behaviors, as distinct from their gonadal physiology, cannot be addressed by us because we never observed mating during the course of this study.

Although this study was conducted during a period of extended drought (1997 to the present) in Hawai'i (U.S. Department of Commerce 1975–2000*b*), our data suggest that the effect of photoperiod in cuing reproductive cycles in *A. sagrei* cannot be ignored. Decreasing photoperiod corresponds with the period of minimum reproductive activity of *A. sagrei* in Hawai'i as well as in Florida and

the Caribbean. Although our data, taken in concert with earlier studies, suggest that decreasing photoperiod may be important in this regard, exactly which environmental cues influence the reproductive cycle of *A. sagrei* in Hawai'i and elsewhere must await long-term, controlled experimental studies.

Qualitative observations by F.K. of newly established *A. sagrei* populations within Honolulu city limits suggest that the population growth potential for this species in Hawai'i is high. Ideally, we would like to quantify this potential to obtain demographic projections at future dates for use in better understanding the invasion process of this highly successful colonizer. Our study begins the process of obtaining the reproductive and demographic data needed to model such growth potential. Currently missing, however, is information on age at first reproduction, length of time required to complete yolk deposition (which combined with our data can provide estimates of average annual fecundity), time of mating (from field observations), and lizard life span estimates. Because *A. sagrei* is still at an early stage of the invasion process in Hawai'i, collection of these data would provide a useful opportunity to test demographic predictions against empirical observations of expansion rate in a relatively short time frame. This may serve, in turn, to better isolate those ecological parameters of greatest importance in assuring successful invasion by lizards, an area of invasion biology that is little studied.

ACKNOWLEDGMENTS

We thank C. Annabel, R. Crombie, T. Kraus, G. Pregill, and E. Teodoro for assistance in collecting, and G. Perry for useful comments on the manuscript.

Literature Cited

Campbell, R. C. 1989. Statistics for biologists. 3rd ed. Cambridge University Press, Cambridge, United Kingdom.

Campbell, T. S. 1996. Northern range expansion of the brown anole (*Anolis sagrei*) in Florida and Georgia. Herpetol. Rev. 27:155–157.

Campbell, T. S., and J. T. Hammontree. 1995. Geographic distribution: *Anolis sagrei* (Brown Anole). Herpetol. Rev. 26: 107.

Dixon, J. R. 1987. Amphibians and reptiles of Texas with keys, taxonomic synopses, bibliography, and distribution maps. Texas A&M University Press, College Station.

Echternacht, A. C., M. A. Wilson, E. J. Michaud, and D. M. MacDonald. 1995. Geographic distribution: *Anolis sagrei* (Brown anole). Herpetol. Rev. 26:107.

Fitch, H. S. 1982. Reproductive cycles in tropical reptiles. Occas. Pap. Mus. Nat. Hist. Univ. Kans. 96:1–53.

Franz, R., G. S. Morgan, and J. E. Davies. 1987. Some recent introductions of reptiles in the Cayman Islands, West Indies. Herpetol. Rev. 18:10–11.

Goldberg, S. R. 1970. Seasonal ovarian histology of the ovoviviparous iguanid lizard *Sceloporus jarrovii* Cope. J. Morphol. 132:265–276.

———. 1972. Reproduction in the southern alligator lizard *Gerrhonotus multicarinatus*. Herpetologica 28:267–273.

———. 1973. Ovarian cycle of the western fence lizard, *Sceloporus occidentalis*. Herpetologica 29:284–289.

———. 1975. Reproduction in the sagebrush lizard, *Sceloporus graciosus*. Am. Midl. Nat. 93:177–187.

Hamlett, G. W. D. 1952. Notes on breeding and reproduction in the lizard *Anolis carolinensis*. Copeia 1952:183–185.

King, K., D. Cavazos, and F. W. Judd. 1987. *Anolis sagrei* (Sauria: Iguanidae) established in southern Texas. Tex. J. Sci. 39:289–290.

King, W., and T. Krakauer. 1966. The exotic herpetofauna of Southeast Florida. Q. J. Fla. Acad. Sci. 29:144–154.

Kishinami, M. L., and C. H. Kishinami. 1996. New records of lizards established on Oahu. Bishop Mus. Occas. Pap. 46:45–46.

Kraus, F. In press. New records of alien reptiles in Hawaii. Bishop Mus. Occas. Pap.

Krusling, P. J., J. W. Ferner, and J. Patterson. 1995. Geographic distribution: *Anolis sagrei* (brown anole). Herpetol. Rev. 26: 108.

Lee, J. C., D. Clayton, S. Eisenstein, and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 1989:930–937.

Licht, P., and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. Univ. Calif. Publ. Zool. 95:1–52.

McKeown, S. 1996. A field guide to reptiles and amphibians in the Hawaiian Islands. Diamond Head Publishing, Los Osos, California.

Minton, S. A., and M. R. Minton. 1984. Geographic distribution: *Anolis sagrei* (brown anole). Herpetol. Rev. 15:77.

Mitchell, J. C. 1982. Geographic distribution: *Anolis sagrei* (brown anole). Herpetol. Rev. 13:80.

———. 1994. The reptiles of Virginia. Smithsonian Institution Press, Washington, D.C.

Platt, S. G., and L. W. Fontenot. 1994. Geographic distribution: *Anolis sagrei* (brown anole). Herpetol. Rev. 25:33.

Schoener, T. W., and D. A. Spiller. 1999. Indirect effects in an experimentally staged invasion by a major predator. Am. Nat. 153:347–358.

Schwartz, A., and R. W. Henderson. 1991. Amphibians and reptiles of the West Indies: Descriptions, distributions, and natural history. University of Florida Press, Gainesville.

Sexton, O. J., and K. M. Brown. 1977. The reproductive cycle of an iguanid lizard *Anolis sagrei*, from Belize. J. Nat. Hist. 11:241–250.

Thomas, R. A., P. J. Thomas, J. Outlaw Coulson, and T. Coulson. 1990. Geographic distribution: *Anolis sagrei sagrei* (brown anole). Herpetol. Rev. 21:22.

U.S. Department of Commerce. 1975–2000*a*. Annual climatological summary. Miami International Airport, Florida. National Climatic Data Center, Asheville, North Carolina.

———. 1975–2000*b*. Annual climatological summary. Kailua, Hawaii. National Climatic Data Center, Asheville, North Carolina.